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Description of *Mediorhynchus papillosus* (Acanthocephala: Gigantorhynchidae) from a Colorado, U.S.A., Population, with a Discussion of Morphology and Geographical Variability

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ABSTRACT: The original description of *Mediorhynchus papillosus* Van Cleave, 1916 included misinterpretations of such taxonomically important structures as proboscis armature. The species was briefly redescribed from Asian material by Schmidt and Kuntz (1977) as well as by various Russian and other workers before and after 1977. The present collection from Colorado provided important taxonomic information previously unreported or erroneously interpreted. The first description of *M. papillosus* from North American specimens collected from a sage thrasher, *Oreoscoptes montanus* Baird, 1858, in Colorado, U.S.A., is presented with new features reported for the first time. A comprehensive comparison of the North American, Asian, and Russian populations is presented and discussed. *Mediorhynchus papillosus* appears to be a geographically variable species, particularly in size of proboscis and its armature, and relative space occupied by the neck and posterior proboscis. The geographically isolated Taiwanese population was markedly different from the Colorado population; the latter was more similar to others from various Soviet republics, particularly the Ukraine. Distinctiveness of geographical populations appears to be related to geographical restrictions, intermediate and definitive host specificity and distribution, and host feeding behavior.

KEY WORDS: *Mediorhynchus papillosus* morphology, *Oreoscoptes montanus*, Colorado, U.S.A., Russia, China, Taiwan, Brazil, Bulgaria.

Van Cleave's (1916) description of 3 imperfect specimens of *Mediorhynchus papillosus* Van Cleave, 1916 was marred by the misinterpretation of proboscis armature. His subsequent treatments (Van Cleave, 1918, 1947) did not contribute additional accounts. Schmidt and Kuntz's (1977) brief redescription, based on specimens from Taiwan and associated Pescadores Islands, corrected some of Van Cleave's interpretations, but lacked information on some taxonomically important structures. It also did not include taxonomic accounts previously reported by other, particularly Russian, observers. The present material from Colorado yielded additional information that is sufficiently new or at variance from published observations to warrant a new treatment of the species.

This report includes the first complete description of the species from the United States, based on new material collected from *Oreoscoptes montanus* Baird, 1858, a sage thrasher. It also includes a comprehensive comparison between the North American, Asian, and East European populations. Type and voucher specimens were examined, and a description of juveniles is provided for the first time. Intraspecific variability among worldwide geographical populations is considered to be a key factor in morphological differences.

Materials and Methods

A total of 27 specimens was collected legally from 1 young road-kill *O. montanus*, 5 km south of Gunnison, 38°32′30″N and 106°56′30″W, 2,438 mi elevation, in the mountains of Gunnison County, Colorado, on 31 July 1995. The bird may have just fledged in June. The body was still warm when first examined. Acanthocephalans were firmly attached to the wall of the small intestine, but did not penetrate into the body cavity. No abnormal inflammation around attachment sites was observed.

Worms were individually teased from the gut wall, extended in refrigerated tap water, and preserved in 70% ethanol. They were later stained in Mayer's acid carmine, dehydrated in ascending concentrations of ethanol, cleared in graduated concentrations of terpineol in 100% ethanol, and whole mounted in Canada balsam.

Measurements are of the longest and widest dimensions. Trunk measurements do not include neck or male bursa. Hooks and spines were measured only in complete profile and counted from at least 2 adjacent rows. This task was made difficult because of the unusually deep cuticular folds within which the almost transparent hooks and spines were embedded. Hook and spine counts in some individuals were problematic

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because of the presence or absence of additional or other hooks as well as because of the slightly spiral arrangement of rows, particularly of spines. Despite these variations, proboscis hooks and spines were arranged in nearly longitudinal rows and were studied, and counted accordingly. Schmidt and Kuntz (1977) made the same observations. Any reference to proboscis hook or spine rows indicates longitudinal rows as observed directly or as converted longitudinal counts from diagonal rows if originally reported as such. Russian workers counted hooks in diagonal rows; their figures were helpful in confirming converted hook/spine counts. All measurements are in micrometers unless otherwise specified. Range is given followed by the mean in parentheses. All juveniles and adults measured were from a single host specimen; measurements do not reflect variability among individual hosts.

The complexities of the praesomal structures and musculature were comparable to those studied by Schmidt (1977), whose terminology is selectively used and/or modified in our work where applicable.

Specimens were deposited at the United States National Parasite Collection (USNPC), Beltsville, Maryland. Specimens examined were borrowed from USNPC and from the University of Nebraska State Museum, Harold W. Manter Laboratory Collection (HWMLC), Lincoln, Nebraska.

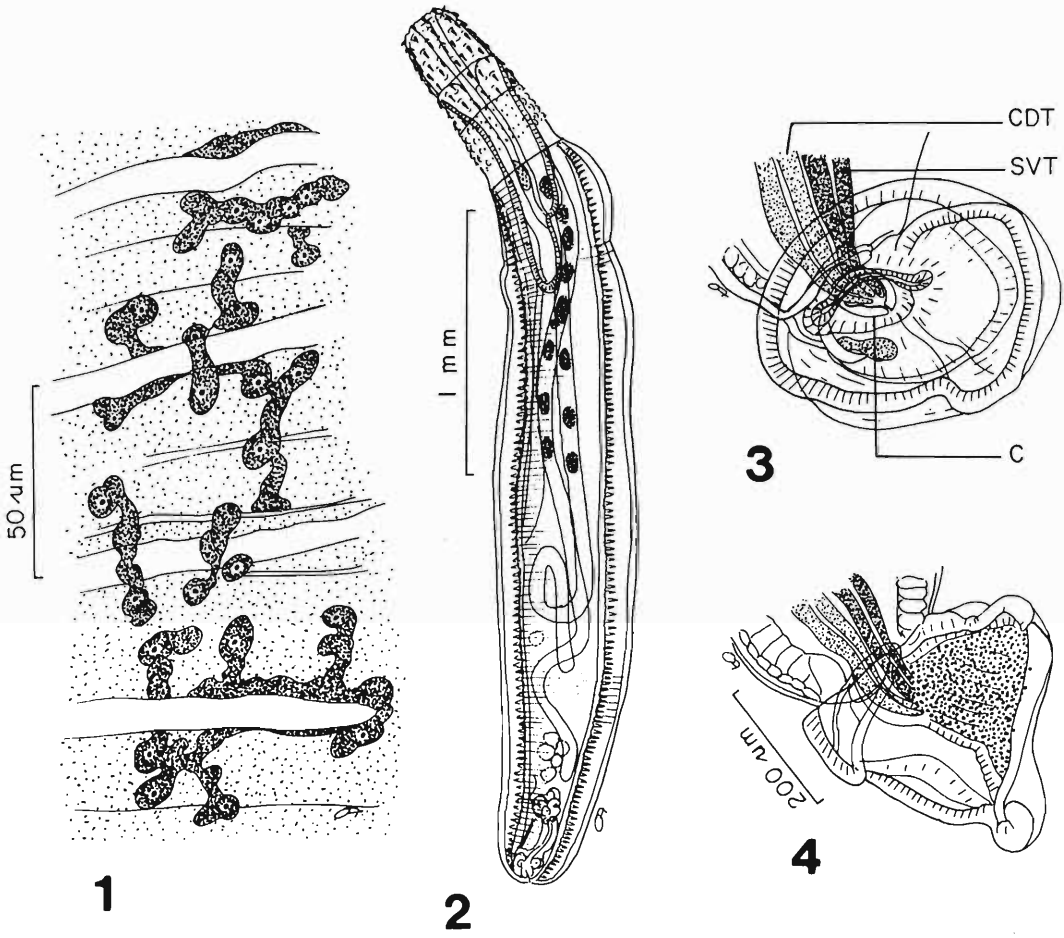
Results

The 27 specimens collected from the single young Colorado sage thrasher included 5 mature males with sperm, 15 females gravid with unripe eggs and ovarian balls (2 with cement plugs), and 7 juveniles (2 males, 5 females). The following descriptions are based on all the Colorado specimens. Measurements are of 4 males, 10 females, and 5 juveniles (1 male, 4 females). Only previously undescribed structures, or those at variance with previous reports, are illustrated.

Mediorhynchus papillosus Van Cleave, 1916 (Figs. 1–10)

GENERAL: With characters of the genus *Mediorhynchus* as described by Van Cleave (1916) and discussed by Schmidt (1977) and Schmidt and Kuntz (1977). Trunk cylindrical, somewhat tapering anteriorly and pointed posteriorly. Juveniles of both sexes with straight trunk, of equal size (2.5–3.0 mm long). Males with straight trunk (6.0–8.0 mm long) and females, with dorsally arched trunk (16.0–21.0 mm long). Sexual dimorphism occurs in all shared structures. These structures are also larger in adults than in juveniles of the same sex. Lacunar system clearly discernible with distinct lateral branches, resembling internal segmentation, spaced at regular intervals. Branches closely spaced in juveniles. Hypodermal nuclei multinucleated, multibranched, amoeboid, often aligned along transverse lacunar branches with terminal ends usually spheroid (Fig. 1).

Proboscis conical, truncate, and thick walled; anterior end flat containing apical organ and sensory pits. Proboscis gradually widening posteriorly into the unarmed neck, divided into 2 parts: anterior part (anterior proboscis) with rooted hooks and posterior part (posterior proboscis) with rootless spines. The posterior proboscis occupies 31–32 (31%) of the total length of the whole proboscis of juveniles, but the length increases to 36–43 (40%) in adult males and 34–41 (39%) in adult females. The 2 parts are clearly separated by a distinct ridge that is NOT marked by the insertion of the proboscis receptacle. Receptacle attached anterior to the separation line just posterior to the insertion of the posterior proboscis inflator muscles in juveniles and slightly more posteriorly in adults (Fig. 5). Hooks and spines are almost transparent and deeply embedded in cuticular folds with only the distal part of blades free to variable degrees (Figs. 6–8). Shape of cuticular folds commensurate with shape, size, and orientation of armature. Those surrounding the hooks are elongate vertically and flat externally, appearing rectangular in profile. Those of spines are crescent or dome shaped and interface with hook folds along the above mentioned ridge. Hooks and spines are arranged in near longitudinal rows that may not regularly alternate. Rows may appear irregular because of the presence of additional hooks or the absence of others as well as because of the slightly spiral arrangement of rows (particularly of spines) in some individuals. Hooks in 18–24 rows each with 4–7 hooks and spines in 26–34 rows each with 4–6 spines. Hooks and spines are largest in females and smallest in juveniles; largest anteriorly and gradually decrease in size posteriorly. Longest anteriormost spines as long as shortest posteriormost hooks. Hook blades sharply curved posteriorly with well-developed powerful roots. Roots are consistently longer than blades, having somewhat less strong broadly rounded proximal end (Fig. 6). Proportion of length of blade to length of root about same throughout anterior proboscis. Spine blades extend out laterally for most of their length and curve sharply posteriorly near their distal end; roots replaced by discoidal tubercles at the proximal end (Figs. 7, 8). Neck well developed with 2 lateral sensory pits

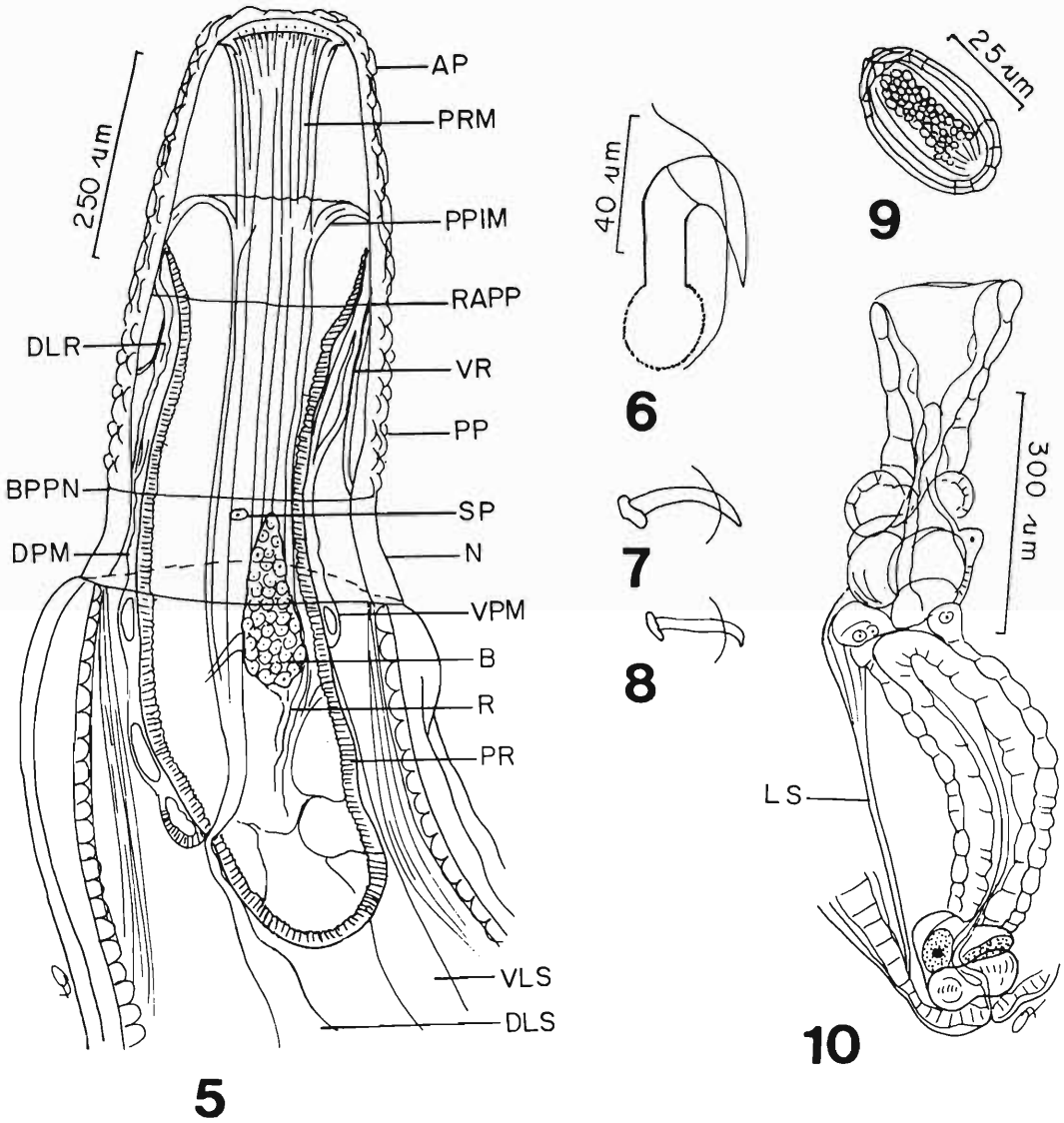


Figures 1–4. ***Mediorhynchus papillosus*** **from** ***Oreoscoptes montanus*** **in Colorado. 1. Branched multinucleated amoeboid hypodermal nuclei in the body wall of a female; clear lateral ducts are transverse lacunar branches. 2. Juvenile female. 3. Ventral view of a bursa showing the terminal portions of the male reproductive system. C, cirrus (penis); CDT, cement duct terminalia; SVT, seminal vesicle terminalia. 4. Lateral view of bursa showing same; stippled portion on top is heavily stained seminal-cement secretions.**

near posteriormost circle of spines, length 22–23% of proboscis of juveniles and adults of both sexes.

Proboscis receptacle (Fig. 5) slightly longer than proboscis in juveniles but ca. 1.5 times as long in adult males and females, complex, single walled throughout except for a short distance at the base of prominent dorsal protrusor muscles. Ventral protrusor muscles, ventral retractors and dorsolateral retractors well developed. Powerful proboscis retractor muscles begin at the anterior end of the proboscis, split dorsoventrally to surround the large ovoid-spindle-shaped cerebral ganglion (brain). Cerebral ganglion located at level of anterior margin of trunk, with larger dorsal branch penetrating the dorsal side of the receptacle a short distance from posterior end. Branched proboscis retractor muscles extend posteriorly as ligament strands to near middle of trunk where they attach to the inner surface of body wall. Near base of the anterior proboscis, exterior fibers of the main retractor muscle mass split laterally, becoming inflator muscles of posterior part of proboscis and attaching to inner wall of proboscis anterior to the ridge separating the 2 proboscis halves (Fig. 5).

Lemnisci long, ribbonlike, usually slightly subequal in length, somewhat broader in anterior half where 5–8 (usually 6) giant nuclei are present. Lemnisci about as long as trunk in juveniles,



Figures 5–8, 10. ***Mediorhynchus papillosus*** **from** ***Oreoscoptes*** **in Colorado. 5. Anatomy of proboscis and receptacle; hooks, spines, and lemnisci not shown. AP, anterior proboscis; BPPN, borderline between posterior proboscis and neck; B, brain (cerebral ganglion); DLS, dorsal ligament strand; DPM, dorsal protrusal muscles; DLR, dorsal lateral retractor; N, neck; PP, posterior proboscis; PPIM, posterior proboscis inflator muscles; PR, proboscis receptacle; PRM, proboscis retractor muscles; R, retina culum; RAPP, ridge between anterior and posterior proboscis, evident upon examination of surface topography where the cuticular folds of hooks and spines interface; SP, sensory pit; VLS, ventral ligament strand; VPM, ventral protrusal muscles; VR, ventral retractor. 6. Hook, root, and cuticular fold near middle of anterior proboscis of a female. 7. Anteriormost spine and fold from posterior proboscis of same female. 8. Posteriormost spine and fold from posterior proboscis of same specimen. 10. Female reproductive system. LS, ligament strand. Figure 9. Egg of** ***Mediorhynchus papillosus*** **from the body cavity of a female from** ***Alauda gulgula wattersi*** **Swinhoe in Taiwan (USNPC No. 74359); note delicate sculpturing and anterior spines of embryo.**

5 times as long as proboscis receptacle in juveniles and adults, and reaching middle of posterior testis in males. Genital opening terminal in both sexes.

JUVENILE FEMALES (based on 4 specimens) (Fig. 2): Trunk with some anterior constriction, but less pronounced than that of cystacanths, 2.50–3.12 (2.772) mm long by 500–690 (580) wide. Whole proboscis 596–660 (634) long; anterior proboscis 406–457 (436) long by 254–381 (305) wide at base; posterior proboscis 190–203 (199) long by 292–406 (334) wide at base. Anterior proboscis with 20–22 (20.7) near longitudinal rows each with 6 rooted hooks; posterior proboscis with 30 near longitudinal rows of 5 rootless spines each. Length of hooks (from anterior to posterior): 38, 35–38 (36), 35, 32, 26–29 (28), 26–29 (27). Length of spines 26, 26, 22–26 (24), 19, 19. Neck 127–152 (140) long by 330–419 (364) wide at base. Proboscis receptacle 711–749 (732) long from insertion to posterior end and 470–533 (512) long from insertion to point of emergence of dorsal retractor muscles by 190–241 (216) wide anterior to emergence and 102–140 (123) wide just posterior to emergence. Cerebral ganglion 165–190 (178) long by 76–89 (80) wide. Lemnisci 2.286–2.794 (2.553) mm long by 89–102 (92) wide. Reproductive system 330–381 (365) long and 12–14 (13%) of trunk length.

JUVENILE MALE (1 specimen): Trunk 2.50 mm long by 590 wide. Proboscis 482 long; anterior proboscis 317 long by 241 wide at base; posterior proboscis 165 long by 254 wide at base. Neck 102 long by 267 wide at base. Anterior testis 241 long by 102 wide; posterior testis 267 long by 127 wide.

ADULT MALES (based on 4 mature specimens with sperm): Trunk 6.80–7.89 (7.510) mm long by 750–870 (810) wide. Proboscis 558–622 (581) long; anterior proboscis 330–381 (349) long by 305–330 (317) wide at base; posterior proboscis 203–254 (231) long by 317–343 (333) wide at base. Anterior proboscis with 19 near longitudinal rows each with 4–6 (5.4) rooted hooks; posterior proboscis with 26–33 (29) near longitudinal rows of 4–6 rootless spines each. Neck 114–140 (127) long by 356–406 (374) wide at base. Proboscis receptacle 838–1,016 (895) long from insertion to posterior end and 610–749 (673) long from insertion to point of emergence of dorsal retractor muscles by 229–254 (241) wide anterior to emergence and 152–229 (197) wide just posterior to emergence. Cerebral ganglion 165–190 (182) long by 76–114 (97) wide. Lemnisci 4.000–4.318 (4.159) mm long by 127–165 (144) wide. Reproductive system in posterior half of trunk. Testes about equal in size; anterior testis 1.206–1.422 (1.279) mm long by 330–419 (378) wide; posterior testis 1.168–1.219 (1.197) mm long by 356–444 (394) wide. Cement glands 8 or 9, orbicular, each with a single large nucleus in a less dense sphere, each 254–406 (318) long by 190–254 (225) wide. Saefftigen's pouch 571 long by 127 wide (n = 1). Seminal vesicle and common cement duct terminate in genital atrium of muscular penis (cirrus) in center of bell-shaped bursa. Bursa 368–381 long by 406–470 wide (n = 2) with well-developed muscular rim and weak ribs (Figs. 3, 4).

ADULT FEMALES (based on 10 specimens gravid with unripe eggs and ovarian balls of which 2 had cement plugs): Trunk 15.60–20.90 (17.684) mm long by 560–840 (688) wide. Proboscis 610–687 (648) long; anterior proboscis 381–444 (397) long by 279–368 (333) wide at base, posterior proboscis 229–267 (250) long by 330–381 (347) wide at base. Anterior proboscis with 18–24 (21.1) nearly longitudinal rows each with 4–7 (5.3) rooted hooks. Posterior proboscis with 29–34 (30.8) nearly longitudinal rows of 4–6 (5.0) rootless spines each. Length of hooks (from anterior to posterior) 32–48 (42), 42–48 (44), 32–48 (40), 32–42 (37), 32–38 (35), 32–35 (33). Length of spines 32–35 (33), 32–35 (33), 26–35 (30), 26–29 (27), 22–26 (24), 22–26 (24). Neck 127–178 (151) long by 394–457 (418) wide at base. Proboscis receptacle 889–1,067 (999) long from insertion to posterior end and 660–851 (740) long from insertion to point of emergence of dorsal retractor muscles by 241–279 (261) wide anterior to emergence 241–267 (257) wide just posterior to emergence. Cerebral ganglion 190–229 (204) long by 102–127 (109) wide. Lemnisci 3.810–5.080 (4.520) mm long by 114–190 (160) wide. Reproductive system robust 864–1,016 long and 5–6 (5%) of trunk length. Vagina and sphincters very well developed. Uterus thick walled, outer layer appears beady, held anteriorly with ligament strand attached to near posterior end of trunk causing it to curve on same side. This is the first report of uterine ligament strands in *Mediorhynchus*. Wall of uterine bell thick, somewhat similar to that of uterus (Fig. 10). Eggs unripe.

Table 1. Morphological variability among geographical populations of *Mediorhynchus papillosus* in selected morphometric characteristics.

	Maryland, U.S.A. Van Cleave, 1916	Colorado, U.S.A. This paper*	Taiwan Schmidt and Kuntz, 1977
Hosts	*Myiochanes virens* *Porzana carolina*	*Oreoscoptes montanus*	*Alauda gulgula* *Alauda arvensis* *Erithaeus calliope* *Dicrurus macrocercus*
Males			
Trunk L × W (mm)	9.3 × 0.75	6.80–7.89 × 0.75–0.87	6.0–9.0 × 0.68–0.70
Proboscis L × W	650 × 300	558–622 × 317–343	350–370 × 240–280
Hooks/row × hook rows	6–7 or 4–6 × 18	4–6 × 19	5–9 × 20–28
Spines/row × spine rows	4–6 × 18 (error)	4–6 × 26–33	3–4 × 45–55
Hook L from anterior	27 (largest)	—	20–28, 20–28, 20–22, 20–22, 20–22, 18–24
Spine L from anterior	—	—	—
Post. prob. L/total prob. L	—	36–43 (40%)	19–30 (26%)†
Neck L/prob. L	—	22%	31%†
Prob. recept. L × W	—	838–1,016 × 229–254	470–500 × 150–180
Anter. testis L × W	—	1,206–1,422 × 330–419	900–1,300 × 300–320
Females			
Trunk L × W (mm)	18.0 × 0.75	15.60–20.90 × 0.56–0.84	11.0–25.0 × 0.72–1.10
Proboscis L × W	650 × 300	610–687 × 330–381	440–510 × 370–400
Hooks/row × hook rows	6–7 × 18	4–7 × 18–24	5–9 × 20–28
Spines/row × spine rows	4–6 × 18 (error)	4–6 × 29–34	3–4 × 45–55
Hook L from anterior	27 (largest)	32–48, 42–48, 32–48, 32–42, 32–38, 32–35	20–28, 20–28, 20–22, 20–22, 20–22, 18–24
Spine L from anterior	—	32–35, 32–35, 26–35, 26–29, 22–26, 22–26	—
Post. prob. L/total prob. L	—	34–41%	22–29 (26%)†
Neck L/prob. L	—	23%	38%†
Prob. recept. L × W	—	889–1,067 × 241–279	520–800 × 200–300
Egg L × W	38–47 × 18–24	—	46–50 × 26–28

* See text for more complete measurements.

† Calculated from available specimens and/or published accounts.

DEFINITIVE HOST: *Oreoscoptes montanus* Baird, 1858, sage thrasher (Mimidae).

SITE OF INFECTION: Small intestine.

PATHOLOGY: None observed.

LOCALITY: Gunnison, Gunnison County, Colorado.

SPECIMENS DEPOSITED: USNPC No. 86963.

ADDITIONAL SPECIMENS EXAMINED (except for specimens from Taiwan and Pescadores Islands, all others are from U.S.A.): From USNPC, No. 6320 (holotype male, allotype female) and No. 6303 (paratype male), No. 74359 (many specimens on 25 slides, Taiwan, Schmidt and Kuntz, 1977), No. 79277 (1 gravid female, Texas), No. 79505 (1 specimen, Colorado), No. 80827 (2 cystacanths, Georgia). From HWMLC, Nos. 34914–34923 (5 males, 8 females on 10 slides, Taiwan), No. 34477 (1 male, Alaska), Nos. 33930, 33931, 34968 (1 male, 5 females, Colorado), Nos. 30276, 30277, 30280, 30281 (1 male, 3 females, Oklahoma), Nos. 30240, 30359 (2 juveniles, unspecified U.S. locations). These are all the specimens that have been deposited in museum collections that were made available for this study.

Discussion

THE TYPE MATERIAL: Van Cleave (1916) described *M. papillosus* (3 specimens) and 2 other species of his new genus *Mediorhynchus* Van Cleave, 1916, which he included with his other new genus *Centrorhynchus* Van Cleave, 1916 in the new family Centrorhynchidae Van Cleave, 1916, because of the insertion of proboscis receptacle at mid-proboscis in both genera. In keying out these new taxa, he distinguished the

Table 1. Extended.

Yakutia, Transbaikal Petrochenko, 1958	Lower Yenesei River, etc. Khokhlova, 1966	Volga, Oren Byrg, etc. Khokhlova, 1986	Ukraine Lisitsyna, 1994	Bulgaria Dimitrova and Genov, 1992
Motacilla alba *Passer domesticus*	*Anthus cervina*	Sparrows and others	Sparrows and others	*Tringa erythropus*
No males				No males
—	7–10 × 0.920–0.995	4.5–10 × 0.68–0.995	6.58–10.04 × 0.56–0.76	—
—	459–579 × 260–381†	430–601 × 210–381†	520–720 × 350–590	—
—	4–7 × 20–24†	4–7 × 20–24†	4–8 × 20–26†	—
—	3–6 × 32–34†	4–6 × 32–34†	5–8 × 42–46†	—
—	31–34	30–40 to 23–40	35–48, 40–45 (2nd) to 28–38 (last)	—
—	15–19	15–20	25–33	—
—	33–34%†	35–37%†	38–40%†	—
—	32–40%†	9–30%	17–22%†	—
—	1,830–2,130 × —	450–2,130 × —	670–1,120 × 180–270	—
—	1,073–1,535 × 306–535	630–1,680 × 300–610	684–1,010 × 250–260	—
Females				
31 × 0.9–1.2	19–33 × 1.22–1.38	11–13 × 0.68–1.38	27.0–36.0 × 0.82–1.13	11.10 × 1.17
630 × 360	534–564 × 273†	450–564 × 273–350†	520–720 × 350–590	586 × 321†
5–7 × 21–24†	4–7 × 20–24†	4–7 × 20–24†	4–8 × 20–26†	6.7 × 22†
5–7 × 32–34†	3–6 × 32–34†	4–6 × 32–34†	5–8 × 42–46†	5–6 × 22–30†
26–30	34–40	30–40 to 23–40	35–48, 40–45 (2nd) to 28–38 (last)	Longest 25–27
16	19–25	15–20	25–33	—
				—
38%†	29–32%†	27–32%†	38–40%†	35%†
22%†	32–34%†	31–37%†	17–22%†	35%†
—	2,430–3,510 × —	520–3,510 × —	670–1,120 × 180–270	2,180 × —
42 × 23	62–68 × 28–40	52–68 × 26–40	60–65 × 40–43	—

closely related *M. robustus* Van Cleave, 1916 as having 24 longitudinal rows of hooks on the proboscis and a maximum diameter: length of body of 1:5 (or 6) as compared to 18 and 1:9 in *M. papillosus* (Van Cleave, 1916). However, he stated that *M. papillosus* has "single layered" proboscis receptacle and that "anterior and posterior regions of proboscis with the same number (18) longitudinal rows of hooks." He described 6 or 7 hooks and 4–6 spines per row, but his figure 6 shows 9 hooks and 6 spines in profile of 1 row. Van Cleave (1916) adequately described other structures (Table 1) and provided sketchy illustrations of a male whose lemnisci extended to the anterior testis, posterior part of male reproductive system with invaginated bursa, barely visible eggs, proboscis surface without hooks, and outline of proboscis and receptacle walls and retractor muscles. Later, Van Cleave (1918) designated *M. papillosus* as the type of the genus *Mediorhynchus*. His original description (Van Cleave, 1916) and 3 illustrations were used as is by Meyer (1932) and Petrochenko (1958, in part). In his review, Van Cleave (1947) provided a tabular key to North American species of *Mediorhynchus* in which he revised the number of *M. papillosus* hooks to 8–10 per diagonal row or 4–6 per longitudinal row, but presented no specific description or additional information. The holotype male (USNPC No. 6320) demonstrates a proboscis receptacle insertion at a level anterior to the separation line between anterior and posterior proboscis, as observed in our material from Colorado. Both holotype and paratype males had 8 cement glands each and contiguous testes.

OTHER U.S. MATERIAL: The other material from Colorado examined (HWMLC Nos. 33930, 33931, 34968) included 4 gravid females and 1 male from the G. D. Schmidt collection and 1

female cystacanth. The females were largely uninformative, but the male was similar to our material, particularly in proboscis and armature characteristics (Table 1). The male specimen from Alaska (HWMLC No. 34477) had a partly retracted proboscis, and accurate observations were not possible. The Oklahoma specimens (HWMLC Nos. 30276, 30277, 30280, 30281) (1 male, 3 females) were poor, contracted, and largely opaque. One female (?) was beyond recognition, but another female had a proboscis that appeared similar to that of our Colorado specimens. Specimens from unknown U.S. locations include a similar female with comparable proboscis to the latter material and 2 unremarkable juveniles (HWMLC Nos. 30210 and 30359, respectively).

Of the 8 species of *Mediorhynchus* occurring in North American birds, *M. papillosus* appears to be the most common; it has been reported in the most number of host species (43) (Nickol, 1977). Most reports, however, present only host and locality records or incidental remarks, e.g., Wallace and Olsen (1966), Nickol (1969), Kayton and Schmidt (1975). The present study represents the first taxonomic treatment of any North American material of *M. papillosus* since its original description in 1916.

NON-U.S. MATERIAL: *Mediorhynchus papillosus* is also well represented in birds from South America, Asia (Taiwan, China, Russia and other former Soviet republics), and Eastern Europe (Bulgaria) and has been described from populations in many of these regions. A distinct degree of morphological variability associated with its geographical populations is clearly evident. Factors related to intermediate and definitive host specificity associated with geographical restrictions, intermediate host distribution, and the apparent lack or scarcity of paratenic hosts possibly are involved. This geographical variability is consistent and is best illustrated by a comparison between the North American population from Colorado described herein and the Asian population from Taiwan. This variability does not appear to be related to host species, because the many specimens we examined from Taiwan (USNPC and HWMLC) were collected from 6 different host species and were consistently morphologically homogeneous.

THE TAIWANESE MATERIAL: The Kuntz collection from Taiwan and associated Pescadores Islands was briefly described by Schmidt and Kuntz (1977), who provided 3 figures of a very small male, female, and proboscis and neck. In spite of their statement that "many specimens . . . from a variety of passeriform birds on Taiwan . . . together with specimens from North America, including type specimens, allow[ed] the . . . redescription" of *M. papillosus,* it is likely that Schmidt and Kuntz (1977) used only Taiwanese material. Our conclusion is based on the complete agreement between their description and our study of their Taiwanese material (USNPC No. 74359). Schmidt and Kuntz (1977) provided a good description; however, it lacked information on some male and female reproductive structures, proboscis receptacle anatomy, sexual dimorphism in proboscis armature, and insertion points. They also did not include other taxonomic accounts previously reported by previous authors, e.g., Petrochenko (1958) and Khokhlova (1966). These, along with other Russian studies of *M. papillosus,* are discussed below. Information from the description of the Taiwanese population relevant to the comparison with our Colorado population is summarized in Table 1. Compared to our specimens from Colorado, those from Taiwan have characteristically and consistently smaller proboscis, proboscis hooks and spines, and proboscis receptacle. They also have more hooks per row but many more rows of spines (45–55) each with only 3 or 4 spines. This results in the posterior proboscis occupying a considerably shorter portion of the proboscis (26%) in males and females and the neck a longer portion (31% in males and 38% in females) (Table 1). The latter percentages were calculated from the Taiwanese material, which provided the additional following information: lemnisci with 6 to 8 giant nuclei in thicker proximal half and extend to middle of posterior testis, males usually with contiguous testes and 7 to 9 (usually 8) cement glands, females of same size as our Colorado females but contained many ripe eggs.

The other Taiwanese material examined (HWMLC Nos. 34914–34923) was part of the G. D. Schmidt collection, which constituted 5 males, 2 young and 6 gravid females that were collected by various Taiwanese workers, mostly between 1958 and 1961 (3 in 1976). These specimens were very similar to the other Taiwanese specimens examined (USNPC No. 74359) and agreed with the description of Schmidt and Kuntz (1977) (see Table 1).

THE FORMER SOVIET REPUBLICS MATERIAL: Belopolskaia (1958) and Petrochenko (1958) were the first to report *M. papillosus* from Russia. Belopolskaia (1958) only recorded the acanthocephalan from white wagtails, *Motacilla alba,* in the Sudzukhinsk reserve during May, July, and September, and noted females reaching up to 36 mm long. Petrochenko (1958) described only females from the same host species as well as from *Passer domesticus* from the collections of the All-Union 100th Helminthological Expedition in Yakutia and the 11th expedition in the Transbaikal area (Table 1). His specimens were very similar to ours from Colorado in proboscis size, relative space occupied by posterior proboscis and neck, and arrangement and number of hooks and spines but not their size; he provided only 1 measurement of each. Petrochenko (1958) recognized that the proboscis receptacle is "one-layered throughout and in the posterior part two-layered on one side." Two discrepancies, however, were made in his original figures. In his figure 129d, the insertion of proboscis receptacle was shown exactly at the level between the anterior and posterior proboscis. In his figure 129e, the proximal end of spines was shown bifurcated and nondiscoidal. In addition, he indicated a surprising number (35–36) of nuclei in each lemniscus.

Khokhlova (1966) described a small collection of male and female *M. papillosus* from *Anthus cervina* in the lower Yenisei River and Norilsk lakes area. She did not observe sexual dimorphism in proboscis armature and provided only 1 measurement each for hooks and spines. Khokhlova's (1966) worms were similar to ours from Colorado in proboscis size, arrangement and number of hooks and spines, and size of hooks, but had a relatively longer neck, a very long proboscis receptacle, and large eggs (Table 1). Several discrepancies are noted: she described, and illustrated (her fig. 7b), a "double-walled proboscis receptacle ... consists of a short thick-walled sac, located inside a long thick-walled sac" (Khokhlova, 1966), clearly mistaking the protrusal muscles for the "outer sac." In the same figure (7b), the proboscis receptacle is shown inserted anterior to the "constriction" between anterior and posterior proboscis (as it should be), while the text indicated insertion at that "constriction." In her figure 7a, she shows a proboscis receptacle not pierced by missed retractor muscles and makes no reference to such muscles anywhere in the text. The female reproductive system (her fig. 8b) does not show any sphincters, and the eggs (her fig. 8c) had thin unsculptured single-membraned shells.

Khokhlova (1978) provided a list of 34 host species of *M. papillosus* in 13 regions of the "USSR." In her expanded review, Khokhlova (1986) redescribed *M. papillosus* listing 45 species of bird hosts from "land along Volga, Oren Byrg Oblast, West Siberia, Yakutiya, Tuva, Seaside, Okhotsky shoreline, Chukotka, Komandorskiye Islands, Ukraine, Georgia, Armenia, Azer Baijan, Turkmen, and Uzbekistan." Worms described by Khokhlova (1986) were similar to those described earlier (Khokhlova, 1966), with some variations in size of trunk, hooks, proboscis receptacle, and relative space occupied by the neck in males (Table 1). Both agree with our description of the Colorado specimens in size of proboscis and hooks, arrangement and numbers of hooks and spines, but their specimens had a relatively longer neck and a very long proboscis receptacle (Table 1). The errors noted above in her earlier description (Khokhlova, 1966) (above) persisted in this one. Her (Khokhlova, 1986) bibliography did not include Schmidt (1977), which suggests that she may have not been privileged to his interpretation of proboscis receptacle musculature and associated structures. New illustrations of hooks and spines, after other authors, poorly represented their form, with hook roots lacking the proximal rounded end and proximal end of spines being forked.

Peresado'ko (1980) described specimens of *M. papillosus* from charadriiform birds in Western Siberia: new host and locality records. His specimens were similar to those described in Bulgaria (see following section).

Lisitsyna (1994) described *M. papillosus* from *Perdix perdix, Glareola pratincola, Alauda arvensis, Hirundo rustica, Sturnus vulgaris, Turdus viscivorus,* and *Silvia nisoria* in Kherson Oblast (Black Sea Biosphere National Park), Crimea, after considering the descriptions of Van Cleave (1916, 1947) and Schmidt and Kuntz (1977). Her material included other *Mediorhynchus* specimens erroneously identified by others as *M. armenicus* Petrochenko, 1958, *M. micracanthus* (Rudolphi, 1819) Meyer, 1932, *M. tenuis* Meyer, 1931, and other previously unidentified material from the Ukraine. In her description, Lisitsyna (1994) reported no sexual dimorphism in the size of proboscis, hooks,

spines, neck, and lemnisci or in number and distribution of armature. Her specimens, however, appeared most similar to ours from Colorado in practically all characters listed in Table 1, with the exception of her longer females, somewhat wider proboscis with more spine rows, and smaller testes. Unfortunately, she described and illustrated (her fig. 1a) a proboscis receptacle that is double walled throughout and "attached at the region of constriction" between anterior and posterior proboscis. Lisitsyna (1994), however, recognized (but did not include in her fig. 1a) the proboscis retractor muscles and their penetration of the proboscis receptacle wall "mediolaterally." Hook roots (her fig. 1b) were poorly depicted and appeared atypical of the species.

Other reports from the former Soviet republics that are not taxonomically or morphologically oriented dealt primarily with new host and/or locality records of *M. papillosus,* e.g., in *Columba livia* in Turkmenia (Meredov, 1976), in *Passer montanus* in European U.S.S.R. (Kostyunin, 1978), in *Falco naumanni* in Azerbaidzhan (Samedov, 1979). No attempt will be made to discuss this literature here.

THE BULGARIAN MATERIAL: In Eastern Europe, *M. papillosus* was recorded from various bird species in Bulgaria by Stoimenov (1962, 1963), Tsacheva (1967), and Tsacheva-Petrova (1971). Dimitrova and Genov (1992) described only 1 female in *Tringa erythropus* from near Bourgas, Bulgaria. Measurements and counts (Table 1) were similar to those of most Russian specimens, especially those of Peresado'ko (1980), except for having smaller proboscis hooks and a larger proboscis receptacle. The ratio of neck length to proboscis length was similar to that reported by Khokhlova (1966, 1986). The number of spine rows was small, but that was questioned by the authors.

OTHER MATERIAL: The non-American distribution of *M. papillosus* extends into South America and beyond the former Soviet republics to China and Taiwan to the east and Eastern Europe to the west. In China, it was reported in Fujian from *Pica pica sercea, Glaucidium cuculcidium,* and *Eurystomus orientalis* by Wang (1966). In Brazil, *M. papillosus* was reported from sparrows, *Passer domesticus,* by Brasil and Amato (1992). The above reports from China and Brazil dealt only with host records.

Conclusions

Mediorhynchus papillosus has a wide distribution outside of North and South America in Asia from Taiwan to the east into China, many of the former Soviet republics, and to Eastern Europe to the west. The present paper represents the first complete description of adults and juveniles in North America. The distribution of proboscis armature is interpreted as being in nearly longitudinal rows. New features, or those that have been previously reported erroneously, are presented and illustrated for the first time. These include (1) the branched, multinucleated amoeboid hypodermic nuclei and their association with the transverse lacunar branches, (2) the anatomy of proboscis receptacle, its associated structures, and its insertion anterior to the ridge between anterior and posterior proboscis, (3) detail of proboscis hooks and spines and the different cuticular folds in which they are deeply embedded, (4) juveniles are described for the first time, (5) terminal male genitalia and bursa described for the first time, (6) female reproductive system properly described and uterine ligament strands described for the first time.

A comparison among the geographical populations of *M. papillosus* indicates its marked variability in certain key characteristics presented in Table 1, with the U.S. population from Colorado and the Taiwanese population being at opposite ends of the variability spectrum. Specimens from Taiwan characteristically had smaller proboscis, proboscis hooks and spines, and proboscis receptacle. They also had a comparatively shorter posterior proboscis with more rows of spines each with fewer spines, more hooks per row in the anterior proboscis, and a comparatively longer neck. It appears as though, within the space available for the proboscis neck region, the distribution of armature becomes a function of how this space is divided between anterior proboscis, posterior proboscis, and neck.

Although all Russian workers interpreted proboscis armature as being in diagonal rows (converted in Table 1) and misinterpreted the proboscis receptacle (except Petrochenko, 1958), its insertion and associated structures, and proboscis armature, their *M. papillosus* material, particularly that from Ukraine (Lisitsyna, 1994), was considerably closer to ours from Colorado than that from Taiwan. Variability is considered

as being geographically, rather than host, related because the many specimens examined from Taiwan were collected from 4 different host species and yet were morphologically homogeneous. Geographical restriction of intermediate (and adult) hosts in the apparent absence or scarcity of paratenic/reservoir hosts is probably a factor contributing to the apparently disjunct distribution of *M. papillosus*. Disjunct populations would promote distinct geographical diversity with consistent morphological difference from each other. The characteristically distinct population of Taiwan is a good case in point, representing an extreme case of disjunction on the island. Taxonomic features of that population render the key of Schmidt and Kuntz (1977) inoperable, at least for *M. papillosus*, where hook length is the major character used in the key.

Van Cleave (1947) was the first to note that "reservoir intermediate hosts are lacking or at least play little role in pyramiding infections of the definitive host." This makes the distribution of adults in the final host totally dependent on the distribution of larval forms in their invertebrate intermediate hosts and on bird feeding behavior. Records of *M. papillosus* larvae are known only from various species of beetles (Coleoptera) of the family Tenebrionidae (darkling beetles) from Uzbekistan and Turkmen (Kabilov, 1969), Crimea (Ivashkin and Shmytova, 1969), and Tajikistan (Gafurov, 1975). Ivashkin and Shmytova (1969) described 1.80–1.87 mm long *M. papillosus* cystacanths that were encysted in the body cavity of *Tenthyria taurica* (most) and *Pimelia subglobosa* (Coleoptera) in the steppe region of Crimea Oblast and noted the corresponding distribution of adults "among sparrows, chickens, and other birds of this area." Khokhlova (1986) described 1.2–1.9 mm and 1.30–1.53 mm long cystacanths that were encysted in intermediate and "reservoir" hosts, respectively. Khokhlova (1986) speculated that reptiles may represent possible "reservoir" hosts.

The intermediate hosts of larval *M. papillosus* in the United States are not known. The stomach of the sage thrasher reported in this study contained small beetle, grasshopper, and sow bug parts. There are over 1,400 North American species of tenebrionid beetles, most of which are of western distribution throughout the arid regions of the United States (Borror and DeLong, 1971). The tenebrionid *Adesmia gebleri* was shown to harbor natural infections of *M. micracanthus* (Rudolphi, 1819) Van Cleave, 1924 in Kara Kum, "USSR" (Ryzhikov and Dizer, 1954). In the United States, the life history of only 2 other species of *Mediorhynchus*, *M. grandis* Van Cleave, 1916 and *M. centrurorum* Nickol, 1969, is known. Moore (1962) experimentally infected the dock beetle, *Castroidea cyanea* (Chrysomelidae), 4 species of grasshoppers, and the cricket *Gryllus* sp. (Orthoptera) with eggs of *M. grandis* that successfully completed development to cystacanth stage, and suggested that first and last host species represented "potential intermediate hosts." Nickol (1977) demonstrated natural and experimental infection of woodroaches, *Parcoblatta pensylvanica* (Blattidae), with *M. centurorum*. Nickol (1977) obtained naturally infected woodroaches from foraging and nesting sites of frequently infected woodpecker definitive hosts, and Jackson and Nickol (1979) reported that nesting site, foraging behavior, and food items apparently limit, in nature, the number of species hosting *M. centurorum*. The above suggestions provide additional support for our contention that the distinctiveness of geographical populations of *M. papillosus* is enhanced by its geographical restriction to habitats containing viable populations of proper intermediate and definitive hosts where parasite transmission is optimized by compatible host specificity and feeding behavior. This is particularly evident in the case of the isolation of the Taiwan and Pescadores Islands population from those of the United States, on the one hand, and of the former Soviet republics, on the other.

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